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Ecological energetics of the millipede, *Xenobolus carnifex* (Fabricius) (Diplopoda: Spirobolida)

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Abstract — Composition and biomass of the millipede, *Xenobolus carnifex* population in two huts of Anaiyur village, Madurai were estimated by direct observation. Data on rates of feeding, assimilation and conversion obtained in the laboratory were applied to estimate the rates and efficiencies of energy flow from the reed (*Aristida sativa*) through the *X. carnifex* population during 1997–2000. Ecological and exploitation efficiencies increased from 0.289 to 0.480% and 19.5 to 33.7% during the study period. An average of 257,947 kJ/m^2/year reed energy was available in the roof. Of this over 25% was channeled through *X. carnifex* population. The millipede delivered over about 69% of the ingested reed energy as feces, which supported coprophagus insects, which coexisted in the roof. The millipede population lost about 30% of the ingested energy on metabolism and converted at the rate of 943 kJ/m^2/year. An energy flow model has been drawn and discussed in the light of information available in the literature.

Key words — *Xenobolus carnifex*, energy flow, rates and efficiencies, energy budget, coprophagus insects

Introduction

One of the important areas of contemporary ecological research is the assessment of energy parameters of ecosystem and populations (Kohler et al. 1987). Laboratory studies on bioenergetics and field studies of population dynamics together provide the basic data required for the estimation of energy flow from producer to the consumer populations. Several workers have estimated the rate and efficiency of energy flow through different trophic levels of invertebrates (McNeill 1971; Axelsson et al. 1974; Delvi & Pandian 1979; Muthukrishnan & Palavesam 1992; Srinivasaperumal 1994). Reichle et al. (1975) reported that the dynamics of functional organization of an ecosystem is based mainly on the manifold interactions between members of a trophic web rather than on the efficiency with which energy is exchanged between trophic levels.

Millipedes are primary consumers on dead organic matter. McBrayer & Reichle (1971) reported that millipedes are litter fragmenters. The contribution of the millipedes to the ecosystem is significant as they transfer energy through their feces and produce animal biomass for the consumption by members of the next trophic level who are called as secondary consumers (Wooten & Crawford 1975). Information available on ecological energetics of millipedes is far less than that is available for several other groups (Satio 1967; Phillipson 1967; O'Neill 1968). Hence, in the present study an attempt has been made to estimate the rates and efficiencies of energy flow and to construct a model for the flow of energy from the roof cover material, the reeds of *Aristida sativa* to *Xenobolus carnifex* population and from it to the other populations in the ecosystem.

Materials and Methods

The study was conducted in two huts located in Anaiyur village, a settlement at the outskirts of Madurai, India (lat 9°58′N and long 78°10′E). The roofs of the huts were two to three years old. Temperature, rainfall and humidity during the study period were recorded. To study the ecological energetics of the population in the roofs of selected huts, consumption and utilization of *A. sativa* reed by *X. carnifex* in the laboratory and population census of the millipede in the field were estimated.

Bioenegetics of X. carnifex

The millipedes were fed *ad libitum* on dry *Aristida sativa* reeds. Following the IBP formula of Petrusewicz & Macfadyen (1970) usually represented as

$$C = F + U + R + P$$

Food energy uptake (C), fecal energy loss (F) due to egestion, and excretion of urine (U) in the form of uric acid, which is inseparable from feces (FU), energy accumulated by way of production or tissue conversion (P) and energy

lost by the individuals due to metabolism (R), derived as the difference between C and sum of FU and P were estimated for the different stages of *X. carnifex* males and females reared at 28, 32, or 36±1°C, 10L: 14D photoperiod and 80 ±5% relative humidity in the laboratory. Food energy assimilated (A) by the individuals was calculated as the difference between energy ingested and energy lost due to egestion of feces and urine (A＝C－FU). All estimations were made in dry weight. Energy densities (J/mg dry weight) of samples of millipede, its food and feces were estimated in a Parr (Moline, U.S.A) 1421 Semi-micro bomb calorimeter. Considering the energy density of the millipede, its food and feces the dry weight data on food consumption, egestion, production and metabolism were converted into energy. Rates of feeding (Cr), assimilation (Ar), production (Pr) and metabolism (Mr) for the different stadia were calculated by dividing the corresponding quantitative values expressed on per individual basis by the mid-body weight (Waldbauer 1968) of the millipede and the duration of the stadium/feeding period in days and presented on Tables 1 and 2. Except the animals belonging to III stadium all the test animals were reared individually in cylindrical plastic terraria (9 cm h×5 cm dia); animals of the III stadium were reared in groups of two. Five replicates were maintained for each life stage. Feeding experiment for the life stages whose duration extended beyond 60 days was carried out on three different weight classes representing the stage and the bioenergetics parameters for the stage were calculated considering the performance of the weight classes during a period of 15 days. The average of the Cr and Ae (Assimilation efficiency) of the three weight classes of a stage are treated as the Cr and Ae of the stage. Relating the Cr to the duration and mid-body weight of the stage, food consumption (C) during the stage was calculated. Considering the Ae of the stage and the C thus calculated, energy loss through feces during the stage was calculated. From the energy equivalents of the animal at the commencement and at the termination of the stage growth during the stage was calculated.

Density and biomass of X. carnifex *population*

The total roof area of the two huts was 120 and 130 m^2. Four quadrates each with an area of 1 m^2 in the four corners of each roof were selected and demarcated with a rope permanently. The selected quadrates could be reached easily through a ladder without damaging the roof. Field study was conducted in the selected quadrates of the roofs for 3 years during October 1997-September 2000. The study was conducted in the roofs on alternate fortnights except during the egg laying period (October-December), when the samples were collected once in a week. Under extreme conditions of habitat degradation due to weathering of the thatch material in the roof, the millipede drops down to the floor in large numbers. Otherwise, under normal conditions, the animal rarely moves from place to place. The total developmental period from egg to sub adult is 256 days; the adult stages (XI and XII) last approximately for about 18 months and the total life span extends approximately to three years.

Eggs, juveniles and adults of the millipede were collected from the selected quadrates of the roofs with the help of a beating tray. The beating tray was made of a piece of strong fabric about 1m square and kept taut by a light wooden frame with a handle. The beating tray was placed below the thatch and animals were dislodged from it by vigorously shaking the bamboo splits over which the bundled reeds are arranged. The animals, fecal pellets and fragments of reed that fell in to the beating tray were brought to the laboratory. The animals were sorted into males and females (from stadium V onwards) as well as different stages based on the number of segments, length and MSW (Mid Segment Width) and enumerated stage wise. Eggs were hand picked from fecal pellets. Data on number of animals belonging to different stadia collected from four quadrates each of two roofs were averaged. The mean of two such censuses collected during successive fortnights of a calendar month was considered as the mean density of the population. Figures 1–3 present data on population density of *X. carnifex* as a function of stadia during 1997–'98, '98–'99, and '99–2000. Population biomass during different months was calculated as the sum of the products of the number of individuals belonging to different stadia and the mid body weight of the respective stadia obtained from the growth curves at an appropriate temperature (28, 32 and 36°C) close to the field temperature.

Energy budget

Food consumption and utilization by the *X. carnifex* population were calculated by applying the following formulae (see Delvi & Pandian 1979) to the laboratory data on food consumption and utilization reported in Tables 1 and 2 and the mean monthly biomass of the population reported in Table 3.

$$C = \frac{Cr \times Mw \times N \times t}{1000 \times a}$$

$$A = \frac{Ar \times Mw \times N \times t}{1000 \times a}$$

$$P = \frac{Pr \times Mw \times N \times t}{1000 \times a}$$

where C, A and P (kJ) are consumption, assimilation and production, Cr, Ar and Pr are the respective rates (kJ/g live wt/day), Mw, mid-body weight (mg) of the individual, N, the mean density (number/m^2) t, the time interval between two successive estimates, a, the area of the field (m^2). Since the rates are calculated per g the 1000 in the denominator remains constant. FU (feces) and R, (metabolism) were calculated from C and A and A and P respectively. Energy budgets were calculated for the period from October, 1997 to September, 2000 and the data are expressed in kJ/m^2/year. During October - February of the study period (1997–2000),

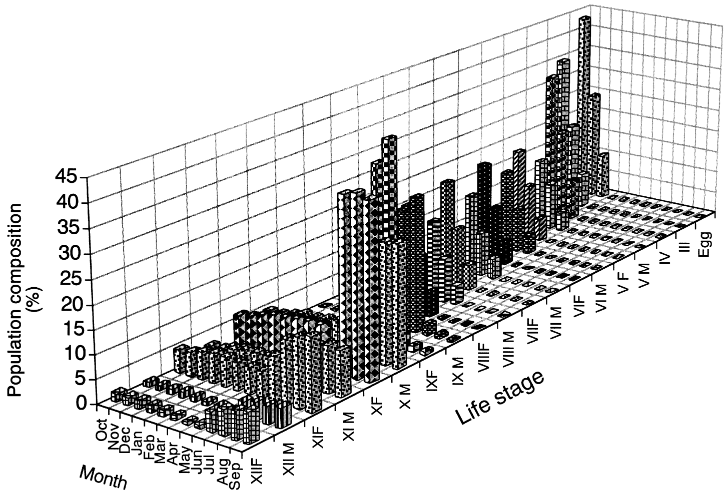

Fig. 1. Percent contribution of different life stages to the population density of *Xenobolus carnifex* during different months of 1997–1998.

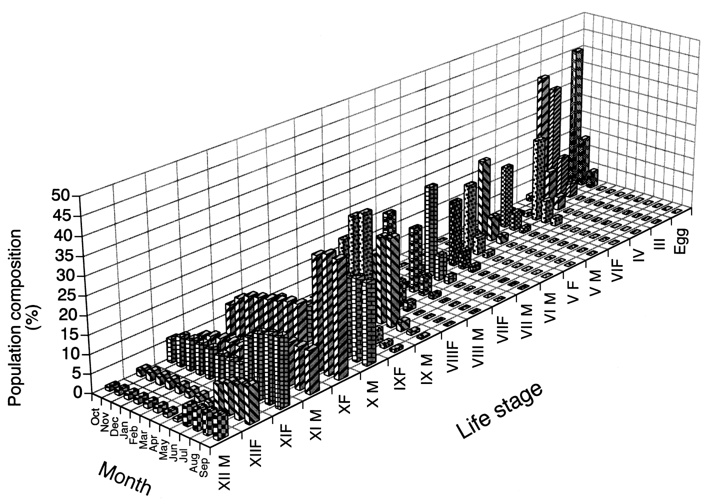

Fig. 2. Percent contribution of different life stages to the population density of *X. carnifex* during different months of 1998–1999.

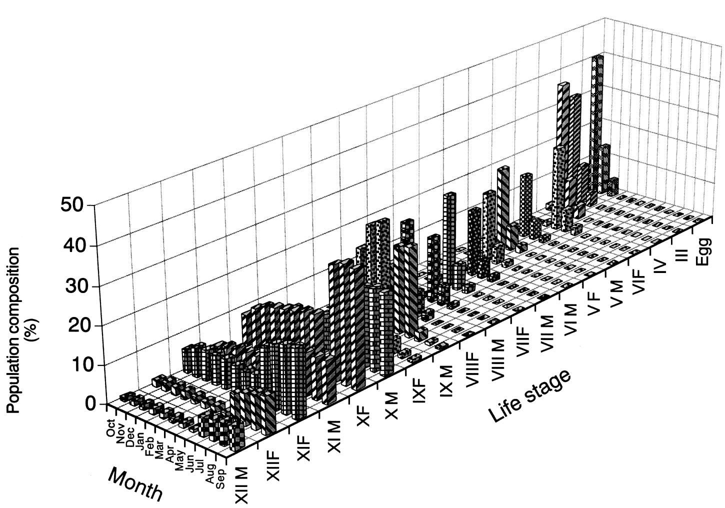

Fig. 3. Percent contribution of different life stages to the population density of *X. carnifex* during different months of 1999–2000.

Table 1. Data on rates of feeding (Cr), assimilation (Ar) and production (Pr) of *X. carnifex* males reared on *A. sativa* reed at the selected temperatures in the laboratory. Each value is the mean±SD of five replicates

Stadium	Cr (kJ/g/day)			Ar (kJ/g/day)			Pr (kJ/g/day)		
	28°C	32°C	36°C	28°C	32°C	36°C	28°C	32°C	36°C
III	52.75±3.2	47.55±2.1	48.74±2.3	19.85±0.9	16.74±0.8	19.38±1.1	1.04±0.2	0.650±0.04	0.689±0.03
IV	35.06±1.9	14.78±0.8	18.88±1.1	12.96±0.8	5.16±0.3	6.45±0.4	0.672±0.2	0.240±0.02	0.276±0.01
V	11.02±0.8	14.45±0.6	13.72±0.8	3.80±0.2	5.78±0.4	4.67±0.3	0.19±0.01	0.217±0.01	0.195±0.01
VI	8.87±0.5	13.77±0.8	11.86±0.4	2.88±0.15	5.32±0.2	4.00±0.08	0.17±0.01	0.196±0.01	0.182±0.01
VII	8.10±0.3	9.69±0.6	8.66±0.4	2.47±0.08	3.49±0.05	2.89±0.03	0.12±0.00	0.113±0.00	0.120±0.00
VIII	6.83±0.3	4.54±0.2	8.26±0.5	2.02±0.05	1.63±0.02	2.66±0.02	0.15±0.00	0.073±0.00	0.133±0.00
IX	3.60±0.2	1.94±0.06	2.37±0.15	1.04±0.05	0.70±0.00	0.75±0.00	0.088±0.00	0.039±0.00	0.049±0.00
X (Sub adult)	0.82±0.03	1.43±0.05	1.50±0.02	0.22±0.00	0.51±0.01	0.45±0.03	0.016±0.0	0.014±0.0	0.019±0.00
XI Adult	0.58±0.02	1.34±0.06	2.36±0.8	0.15±0.01	0.41±0.02	0.70±0.03	0.006±0.0	0.007±0.0	0.009±0.0
XII	0.69±0.02	1.30±0.08	2.11±0.15	0.17±0.01	0.38±0.02	0.59±0.02	0.004±0.0	0.010±0.0	0.011±0.0

Table 2. Data on rates of feeding (Cr), assimilation (Ar) and production (Pr) of *X. carnifex* females reared on *A. sativa* reed at the selected temperatures in the laboratory. Each value is the mean±SD of five replicates

Stadium	Cr (kJ/g/day)			Ar (kJ/g/day)			Pr (kJ/g/day)		
	28℃	32℃	36℃	28℃	32℃	36℃	28℃	32℃	36℃
III	52.55±3.05	47.55±2.3	48.74±1.9	19.85±0.73	16.74±1.11	19.38±0.75	1.043±0.06	0.650±0.03	0.690±0.04
IV	35.00±1.8	14.78±0.9	18.88±1.1	12.96±0.9	5.16±0.35	6.45±0.38	0.672±0.05	0.240±0.01	0.276±0.0
V	9.00±0.4	13.00±0.8	12.84±0.6	3.31±0.19	4.32±0.23	4.02±0.22	0.238±0.04	0.234±0.02	0.191±0.01
VI	7.46±0.02	11.79±0.082	10.20±0.65	2.65±0.11	3.86±0.18	3.07±0.11	0.125±0.01	0.182±0.01	0.175±0.01
VII	6.68±0.45	8.18±0.48	7.80±0.35	2.29±0.125	2.64±0.150	2.29±0.105	0.127±0.01	0.105±0.00	0.119±0.00
VIII	5.73±0.35	3.91±0.17	7.12±0.32	1.94±0.07	1.19±0.02	2.03±0.05	0.134±0.01	0.073±0.00	0.122±0.00
IX	3.56±0.18	1.71±0.06	2.10±0.04	1.16±0.01	0.514±0.02	0.572±0.03	0.077±0.00	0.035±0.00	0.044±0.00
X (Sub adult)	0.82±0.03	1.35±0.01	1.39±0.01	0.244±0.00	0.399±0.00	0.363±0.00	0.018±0.00	0.013±0.0	0.016±0.0
XI Adult	0.55±0.03	1.49±0.02	2.07±0.05	0.157±0.00	0.432±0.02	0.530±0.03	0.006±0.0	0.006±0.0	0.012±0.0
XII	0.45±0.02	1.40±0.08	1.34±0.08	0.138±0.00	0.404±0.03	0.338±0.02	0.005±0.0	0.010±0.0	0.005±0.0

Table 3 Contribution by the different stages to the biomass of *X. carnifex* population in the study area during 1997–2000. Each value represents the mean (X±SD) of four quadrates each of two huts.

Stage	1997–'98	1998–'99	1999–'00
Egg	0.31±0.03	0.28±0.03	0.25±0.02
III	1.27±0.12	1.17±0.18	1.01±0.09
IV	2.59±0.24	2.39±0.22	2.05±0.21
V	5.34±0.58	4.89±0.46	4.24±0.37
VI	10.16±0.99	9.2±0.88	8.19±0.81
VII	17.28±1.23	15.64±1.30	14.19±1.11
VII	30.64±2.56	27.71±2.51	24.84±2.48
IX	151.22±2.10	136.67±11.25	132.33±12.54
X (Sub adult)	567.65±48.64	782.6±60.25	662.1±55.65
XI (Adult)	448.19±39.89	494.21±44.11	568.27±52.22
XII	166.42±11.25	176.02±12.56	231.76±20.13
Total	1401.07±138.77	1650.76±162.93	1648.49±159.57

the average monthly temperature was between 25.8 and 28.5°C, whereas it ranged from 30.7 to 32.9°C during April–July. In March, August and September the temperature fluctuated between 28.8 to 30.0°C. To calculate the energetics parameters of *X. carnifex* population in the field from October to February, and April to July, data obtained in the feeding experiments at 28 and 32°C respectively, were considered. The average of the values obtained at 28 and 32°C were considered for the March, August and September.

Rate of energy flow

Rates of energy flow were calculated by dividing the total energy consumption, energy assimilation, excretion, growth and metabolism of both male and female of all the stadia by the total biomass (g live wt.) of the respective years and expressed in kJ/g/m^2/year.

Ecological energetics

Efficiency of energy transfer from one trophic level to another was calculated by considering the energy available in the study area. Reed energy available was calculated by multiplying the energy content of the reed by the average weight of reed in one m^2 and the values were expressed in kJ/m^2/year. Since the thatching material of the roof has not been changed during the study period; it is assumed that no fresh input of energy occurred during successive years. Due to consumption of reed by the population, considerable

energy is lost by the system every year. Therefore, energy available for consumption by the population at the commencement of successive years was obtained by subtracting the energy consumed by the population during the preceding year from the energy available at the commencement of the year. Efficiencies of energy flow were calculated by using the following formulae:

$$\text{Production efficiency (\%)} = \frac{\text{Production}}{\text{Consumption}} \times 100$$

$$\text{Exploitation efficiency(\%)} = \frac{\text{Consumption}}{\text{Reed energy available}} \times 100$$

$$\text{Ecological efficiency (\%)} = \frac{\text{Production}}{\text{Reed energy available}} \times 100$$

Results

Figures 4–6 present data on monthly contributions to the annual energy budget of the *X. carnifex* population as a function of sex. In general females contributed more to the flow of energy than males and the flow of energy was greater in March compared to other months. Annual energy budget of the population for the years 1997–98, 1998–99 and 1999–2000 has been provided in Table 4. Food consumption by *X. carnifex* population was higher (67810 kJ/m^2/year) during 1998–1999 than that in 1999–2000 (65040 kJ/m^2/year) and 1997–1998 (61540 kJ/m^2/year). Correspondingly, feces egested, energy assimilated, converted and metabolized were also less during 1997–98 and 1999–2000.

Considering the biomass (g live wt/m^2) of *X. carnifex* population and the total energy transferred through the population to various structural and functional components, rates of energy flow for the years 1997–98, 1998–99 and 1999–2000 were calculated and provided in Table 5. During these years the biomass of the population varied between 1401 to 1651 g/m^2 and the population consumed the reed energy at the rates ranging from 39.5 to 43.9 kJ/g/m^2/year. The population converted the assimilated energy at a very low rate (0.562 to 0.651 kJ/g/m^2/year), as it metabolized the energy at rates (11.60 to 13.11 kJ/g/m^2/year) just less than the assimilation rates (12.2 to 13.8 kJ/g/m^2/year). The population channeled its fecal energy through coexisting coprophages at about 69% of the rate of food consumption.

Table 6 presents data on ecological energetics of *X. carnifex* population for the period 1997–2000. At the commencement of the study 3,15,840 kJ/m^2/year was available in the form of *A. sativa* reed. Consequent to the consumption of the reed by the *X. carnifex* population, reed energy available to the population successively decreased to 2,65,220 and 1,92,780 kJ/m^2/year in 1998–99 and 1999–2000. The population exploited the energy available during these years, with efficiencies of 19.5, 25.6 and 33.7% and converted with ecological efficiencies of 0.289, 0.374 and 0.480% respectively. Production efficiency of the population varied between 1.42 and 1.48%. The exploitation and ecological efficiencies of the population averaged 26.3 and 0.381%.

Figure 7 summarises the flow of energy through the roof ecosystem inhabited by *X. carnifex* population. Of 257,947 kJ of energy available per square meter of the roofs, about 25% of is passed through the millipede population; 1.7% of it is passed in the form of fecal energy to coexisting coprophages and microbes and 0.037% to carnivorous reduvids and partly to produce the next generation. The population utilized about 7.4% of the available energy for metabolism.

Table 4 Annual energy budget of *X. carnifex* population for 1997–2000. Values are expressed in kJ/m^2/year

Year	C	FU	A	P	R
1997–98	61540	42264	19276	911	18365
1998–99	67810	46764	21046	992	20053
1999–00	65040	44990	20050	926	19124

Discussion

Information on energy relations of millipedes is essential for an understanding of the energy dynamics of the ecosystem concerned (O'Neill 1968). However, almost very little

Table 5 Rates of energy flow through *X. carnifex* population during 1997–2000. Values are expressed in (kJ/g/m^2/year)

Year	Biomass (g/m^2)	C	FU	A	P	R
1997–98	1401.1	43.9	30.2	13.8	0.651	13.11
1998–99	1650.8	41.8	28.3	12.7	0.601	12.15
1999–00	1648.5	39.5	27.3	12.2	0.562	11.60

Table 6 Ecological energetics of *X. carnifex* population in the roofs of the chosen huts in Anaiyur village

Year	Biomass (g/m^2/y)	Reed energy available(kJ/m^2/y)	Consumption (kJ/m^2/y)	Production (kJ/m^2/y)	Production efficiency (%)	Exploitation efficiency (%)	Ecological efficiency (%)
1997–98	1401	315840	61539	911.4	1.48	19.5	0.289
1998–99	1651	265220	67809	992.4	1.46	25.6	0.374
1999–00	1649	192780	65040	926.0	1.42	33.7	0.480
Mean±SD	1567±144	257947±61852	64796±3142	943.3±43.2	1.45±0.03	26.3±7.15	0.381±0.095

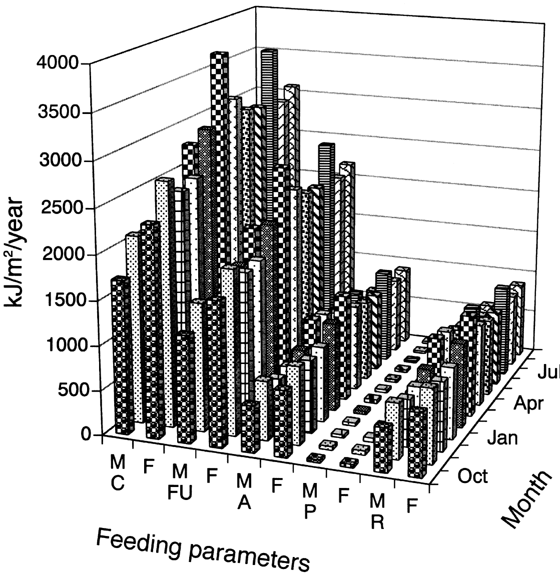

Fig. 4. Monthly contribution to the annual energy budget of *X. carnifex* during 1997–1998.

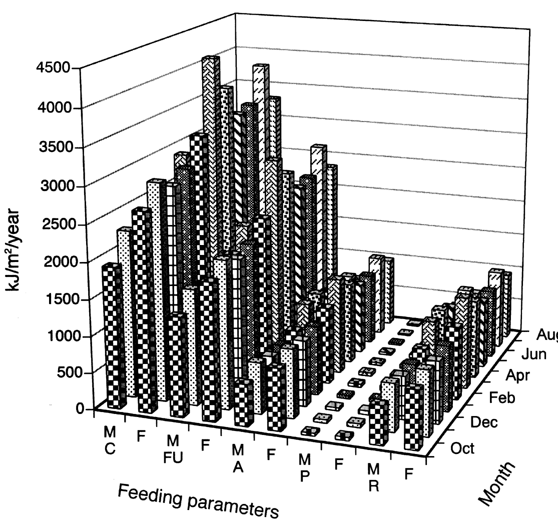

Fig. 5. Monthly contribution to the annual energy budget of *X. carnifex* during 1998–1999.

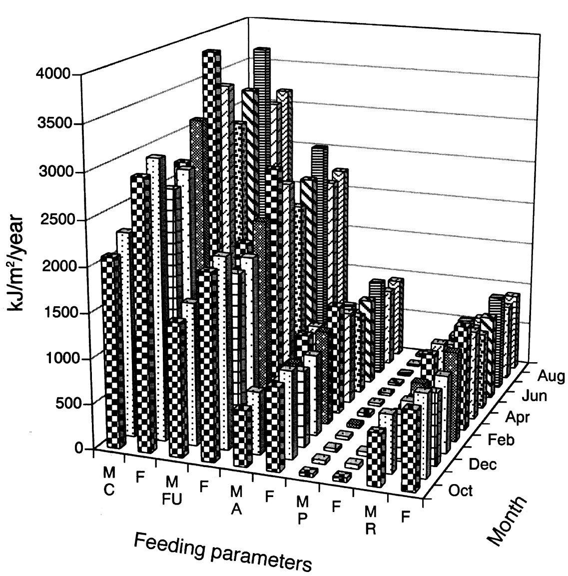

Fig. 6. Monthly contribution to the annual energy budget of *X. carnifex* during 1999–2000.

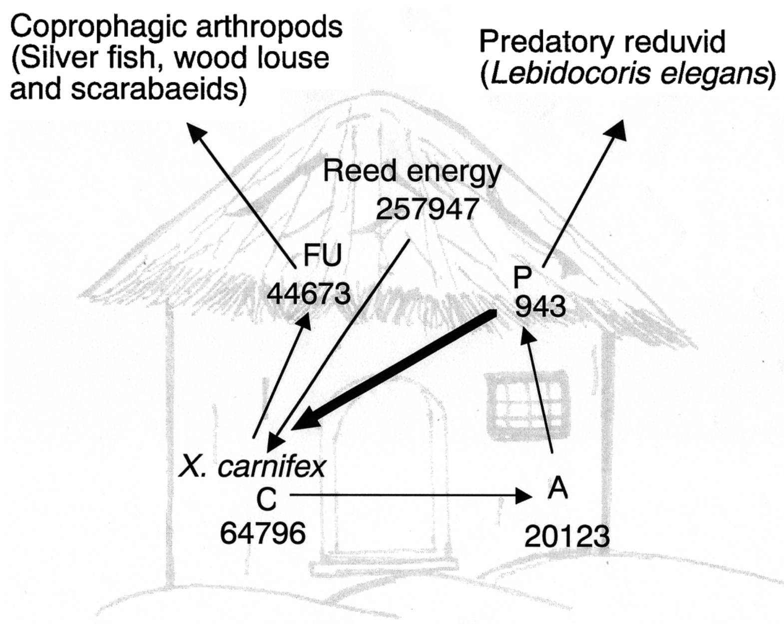

Fig. 7. Energy flow through *X. carnifex* population in the roof of huts during 1997–2000. C=Consumption; A=Assimilation; P=Production (Growth); FU=Feces and Urine. All values are in kJ/m^2/year. Flow into next generation is represented by a heavy line.

information is available on energy flow through millipede populations (Reichle 1967). The present study on *X. carnifex* populations adapted to the xeric conditions prevailing in the roof of huts provides several interesting information. The ecosystem has abundant source of energy in the form of *A. sativa* reeds. The energy is not replenished and is utilized mostly by the millipede population and partly probably by lignolytic microbes.

Xenobolus carnifex is a slow growing millipede with a life span of about three years when it passes through ten immature stadia. Alagesan (2002) reported that food consumption of the millipede varies significantly with temperature and between different stadia. Data on monthly contributions to the annual energy budget of the population pointed out that females consumed more energy than males and during March considerably more energy is passed through the population. During March the reeds on the roof is neither too wet nor too dry, which renders it more suitable for utilization because of the rich culture of lignolytic bacterial population harbored by the reed (Alagesan et al 2003). Such differences are due to the changes in the composition and density of the population during the different months as well as the variations in the feeding rates of the individuals due to changes in temperature.

The *X. carnifex* population displayed mean exploitation efficiency ranging from 19.5 to 33.7% with a mean of 26.3%. Maria Anthoniammal (2003) reported exploitation efficiency of 2.8, 4.3 and 3.2% for the millipede *Aulacobolus newtoni* exploiting *Coffea arabica* in Palni Hills during 1998–'99, '99–'00 and '00–'01. The remarkably high exploitation efficiency of *X. carnifex* population reported in the present study is due to the abundant source of energy in the form of reeds available in the habitat as well as almost negligible cost of foraging by the millipede. In addition the population is subjected to a 'no choice' situation in the habitat, where no other feed material is available. Ecological efficiency of *X. carnifex* in the present study ranged from 0.289 to 0.480% during 1997–2000. Interestingly, very low gross production efficiency ranging from 1.42 to 1.48% was recorded for the millipede population in the present study; it converted 943 kJ/m^2/year; part of this was channeled to the predator population such as reduvids. The population delivered 44,673 kJ/m^2/year (which is 69% of the reed energy ingested) by way of egestion, which supported the life of coprophagic insects such as silverfish, woodlice and scarabaeid beetles. Similarly, Crawford (1978) reported that over 67% of the ingested food (13,712 kcal/ha.) was egested as feces (9,187 kcal/ha.) by the desert millipede, *Orthoporus ornatus* in the feeding season, which lasted for 131 days in Big Bend Park, Texas. Wooten & Crawford (1975) reported that *O. ornatus* exploits the food more efficiently; the feces egested which is as much as 69% of the ingested energy formed a substantial energy source for decomposer organisms. O'Neill (1968) reported that two populations of *Narceus americanus* inhabiting the woodlands in Central Illinois returned about 85% of the ingested energy (10.92; 15.03 kcal/m^2/yr) through feces (9.20; 12.82 kcal/m^2/yr).

Unlike the natural ecosystem, the man-made ecosystem in the roof of huts has the reed made available by man as the source of energy for *X. carnifex* population, the egesta of which sustains the populations of coprophages; a thin population of carnivores survives feeding on the eggs and young ones of *X. carnifex*. As the reeds decompose and deteriorate the whole ecosystem is discarded and used as manure. When the roof is replaced, young ones hatched from the eggs in the soil near the huts colonise the roof and a new cycle is started. This study has thus shown the importance of *X. carnifex* population in recycling a significant proportion of the energy available in the peculiar ecosystem

through coprophages.

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